

THE STRUCTURES INVOLVED IN THE PRESENTATION OF POLLEN TO
VISITING INSECTS IN THE ORDER CAMPANALES.

By R. C. CAROLIN, University of Sydney.

(Plate ii; five Text-figures.)

[Read 27th July, 1960.]

Synopsis.

A comparison of the structures within which pollen is presented to visiting insects in the families Campanulaceae, Goodeniaceae and Stylidiaceae is made. It is shown that the indusium of the Goodeniaceae is not homologous to the pollen collecting hairs of the Campanulaceae. The indusium consists of an upgrowth from the style immediately below the stigmatic branches, variously modified. In *Leschenaultia* the stigmatic function is transferred to the outer surface of the upper lip of this indusium. Furthermore it is noted that in the Stylidiaceae pollen is invariably presented whilst still contained within the anther loculi. The term "pseudo-indusium" is proposed for the compound structure in the Lobelioideae consisting of connate anthers, closed stigmatic branches and stylar hairs. The results suggest that the Order may not be monophyletic. It is suggested that the naked presentation in Campanuloideae developed in drier climates and an intrusion into wetter conditions may have been the selective factor operating to produce the protected presentation of Lobelioideae and Goodeniaceae.

The Order Campanales as constituted by Hutchinson (1926) is characterized by the presentation of the pollen in, or on, certain structures directly associated with the style. The sole exception appears to be *Donatia*, in the Stylidiaceae, in which pollen is presented directly from the anther lobes which are free from the style. It is primarily the similarity in situation of these structures which has been responsible for uniting the three families, usually with the inclusion of Calyceraceae and Compositae, in the Order Campanales (Campanulales or Campanulatae) (see Rendle, 1938).

CAMPANULACEAE.

The pollen-collecting hairs of the Campanulaceae have received considerable attention in the past. These hairs are situated at various positions on the style, the anther lobes, at anthesis, being closely applied to the style. With the growth of the style and the shrinkage of the stamens, or both, pollen is brushed from the anther lobes by the pollen-collecting hairs. These hairs, moreover, at this stage commence to collapse and, in some genera, to invaginate into the large bulbous base. This is particularly marked in *Campanula* (Brongniart, 1839; Hassall, 1842). The latter author has suggested that the collapse, etc., is due to extraction of "juices" (water), and this seems quite feasible. Knuth (1909) remarks that the collapse makes it easier for the pollen grains to be dislodged by visiting insects, and this is the author's experience with *Campanula*, *Wahlenbergia*, *Phyteuma* and *Specularia*. This form of pollen presentation is fairly constant throughout the family with various modifications. The most important point to note is that the pollen collecting hairs are formed from a single epidermal cell (Text-fig. 3, C; Plate ii). The plate shows that in *Campanula* most of the epidermal cells undergo a tangential division to form a hypodermis, those destined to form pollen-collecting hairs do not, however, and subsequently undergo considerable basal enlargement.

The most interesting departure from this general scheme is shown in certain sections of *Phyteuma*; *P. orbiculare* was the species examined. Knuth (1909) states that the pollen is deposited upon the style in the usual manner, but when the filaments shrivel the top of the corolla forms a closed tube around the style. Furthermore, the lower parts of the corolla lobes become free whilst the upper parts remain coherent

and pressing the pollen onto the style. It seems that the upper tube and style are stuck very tightly together, and also that the corolla is growing much faster than the style; the consequence is that the lower, free parts of the corolla-lobes bend outwards. Knuth considers that the style now elongates, carrying pollen upwards, scouring it out of the tube. The mechanism, however, is a little more subtle than that. There is a considerable period in the life of each flower when the corolla is retaining the style and the whole structure appears to be in a state of tension. The style is lying loosely in the tube at this stage, probably due to the collapse of the pollen-collecting hairs. Insects, and Knuth cites the fairly heavy bee and bumble-bee, visiting the flower alight or crawl onto the lower curved part of the corolla-lobes. This forces the upper, tubular part downwards, splitting the coherent tips and exposing the pollen-covered closed stigmatic lobes and style. Subsequently the style elongates and the stigmatic lobes recurve and become receptive.

Thus, in those *Phyteuma* species allied to *P. orbiculare*, i.e., sections *Hedranthum* and *Synotoma*, an increase in efficiency of pollen use has been evolved. The pollen is actually retained within a structure until its deposition onto an insect is imminent. This represents a general phylogenetic trend in the Campanales, as will be shown later, and there seems no reason why the term "pseudo-indusium", proposed below for a similar structure, consisting of different morphological units, in the Lobelioideae should not be extended to the corolline "pseudo-indusium" of *Phyteuma*.

In the Lobelioideae the pollen-collecting hairs are concentrated onto the stigmatic branches, often more or less in a ring. In this case the pollen is presented in a structure compounded of the anthers as walls and the hair ring and closed stigmatic branches as the floor. The pollen is shaken out of this structure by agitation of the hairs on the apex of the anthers (Text-fig. 3, D). When the stigmatic branches are opened and are eventually exerted from the anther tube the pollen is probably no longer viable. Thus, in the species that have been examined, *Lobelia syphilitica* L., *L. gracilis* R.Br., *L. alata* Labill., *Laurentia fluviatilis* (R.Br.) E. Wimm., *L. petraea* F. Muell., the hairs do not act strictly as a brush; in fact they form a "pseudo-indusium" (see below and Text-fig. 5).

GOODENIACEAE.

In the Goodeniaceae it is the indusium or pollen-cup at the top of the style in which the pollen is presented to visiting insects. Brough (1927) and Hamilton (1894, 1895) have described the pollinating mechanism. This involves dehiscence of the anthers in the bud and the deposition of the pollen within the indusium as the latter grows upwards between the connivent or coherent anthers. Pollen is pushed out of the indusium as the stigmatic surface grows and matures.

The microscopic structure of the indusium has not previously been described. Four main types of indusium are to be found within the family, based upon cellular type and the presence and position of hairs.

In *Leschenaultia* the two main lips of the indusium consist of somewhat elongated cells with thin walls. These cells are indistinguishable from the other cells of the style by the nature of their cell-walls (Text-fig. 1, B). The elongated cells are surrounded by an epidermis of more or less cubical cells, some of which, on the outer surface, are minutely papillose. The epidermal cells on the margins of the lips project as long hairs which function as a pollen brush, dislodging pollen from the dehiscent anther lobes so that the tetrads fall into the indusium. The style has a central canal which is, apparently, always open at its upper end into the indusium and at its lower end into the ovary cavity. The upper opening is usually constricted by two large swellings at the base of the indusium (Plate ii). The position of the stigmatic surface presents a problem. Pollen tetrads, in fact, only germinate when they come into contact with the minutely papillose epidermal cells on the outside of the upper lip (Plate ii). Darwin (1871) was the first to note this and it was confirmed in this investigation for *L. biloba* and *L. formosa*. The indusium develops as a rim around the concave summit of the style. This rim gradually expands into the mature, bilabiate

structure. The styler canal does not become visible until fairly late in development (Text-fig. 2, H-J).

In *Dampiera* and *Anthotium* the indusium consists of an outer layer of relatively thin-walled epidermal cells which do not bear hairs except at the base. Beneath this

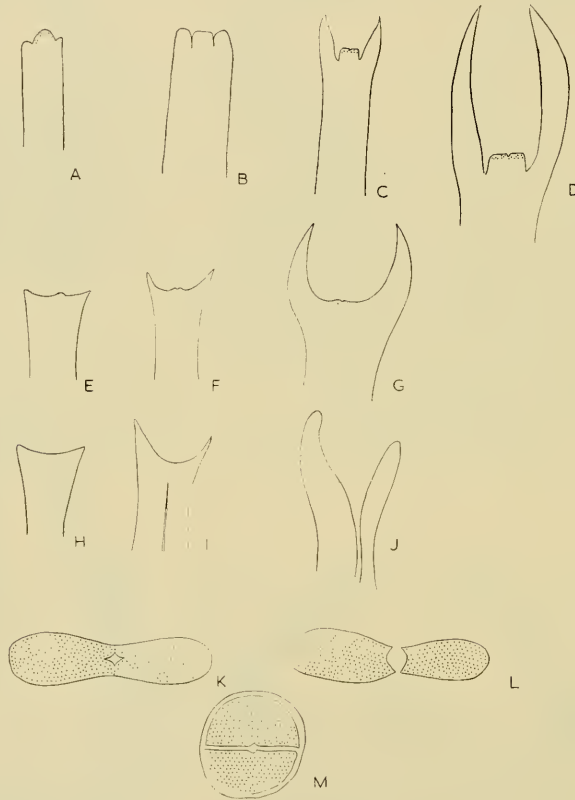


Text-fig. 1.—A, *Dampiera linearis* R.Br. indusium l.s. $\times 100$. B, *Leschenaultia biloba* Lindl. indusium l.s. $\times 100$. C, *Goodenia paniculata* Sm. indusium l.s. $\times 100$.

epidermis there are a number of vertical rows of elongated cells with thick walls and deep pits (Text-fig. 1, A). The stigmatic surface is apparently limited to the edges of a furrow running across the floor of the indusium, morphologically parallel to the position of the ovary septum or its postulated position (see Carolin, 1959, and Brough, 1927) (Text-fig. 2, M; Plate ii). As the stigmatic surface grows it still remains limited

to the edges of the cleft. In some species of *Dampiera* the indusium is 4-lobed and in others 2-lobed (see Hamilton, 1894, 1895) and in still others entire. It arises as a rim on the concave summit of the young style, in the centre of which is a small protuberance, and grows upwards into the mature structure (Text-fig. 2, E-G). The inner, thickened cells of the indusium are formed by both periclinal divisions of the epidermis and anticlinal divisions of the subsurface layers (see Text-fig. 3, A and B).

In *Brunonia* the upper part of the indusium has the same cellular structure as that of *Dampiera*, except that the epidermal cells are often projected into long hairs, although these latter do not occur on the margins of the lips. In the lower parts of the indusium the cells are more normally parenchymatous, shorter and with scarcely

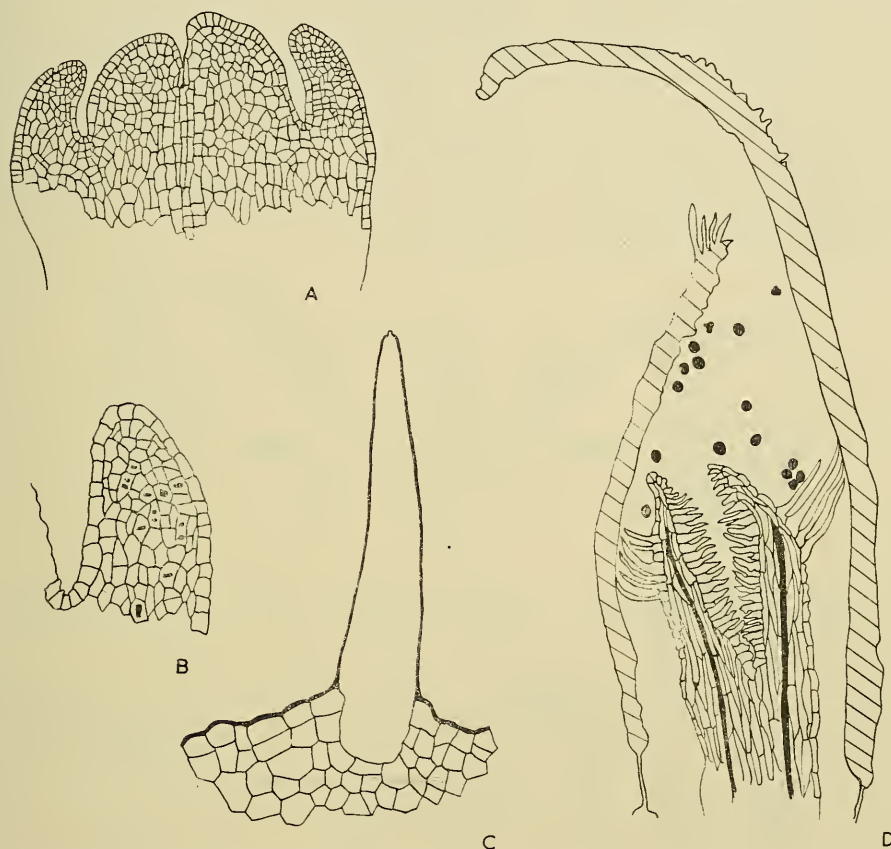


Text-fig. 2.—A-D, Development of the indusium of *Goodenia paniculata* Sm. $\times 25$. E-G, Development of the indusium of *Dampiera stricta* R.Br. $\times 25$. H-J, Development of the indusium of *Leschenaultia biloba* Lindl. $\times 25$. K-M, Surface view of stigmatic surface: K, *Goodenia ovata* Sm.; L, *Goodenia paniculata* Sm.; M, *Dampiera stricta* R.Br.

thickened walls (Text-fig. 1, D); it is bilabiate. The stigmatic surface is apparently limited to the edges of a cleft which extends across the top of the column in the indusium. This cleft is morphologically parallel to the ovary septum. The development of the indusium is similar to that noted in *Dampiera*.

In the remaining genera that have been studied (*Velleia*, *Goodenia*, *Scaevola*, *Selliera*, *Verreauxia*) the indusia are similar. The epidermis consists of relatively thin-walled cells which are often elongated and which may project into hairs, especially on the margins. The inner cells are elongated, arranged in vertical rows, and have much thickened walls with prominent pits (Text-fig. 1, C). Some cells on the outside near the base may be relatively isodiametric with unthickened walls. The indusia may be

4-partite as in some *Velleia* or 2-partite as in some *Goodenia* or entire (see Krause, 1912). There is often a canal in the stigmatic column the shape of the opening of which gives the impression of the stigmatic surface having been originally 4-lobed (Text-fig. 2, K-L). The union of these four lobes, which may correspond to the postulated ancestral 4-carpellary condition of the ovary, has led to the almost uniform stigmatic surface of many species. In some, however, it is the cleft at right angles to the ovary septum which has become emphasized, e.g., *Goodenia pusilliflora*, *Calogyne berardiana* (Carolin, 1959), *G. paniculata* (Text-fig. 2, L), rather than the one parallel to the septum as in



Text-fig. 3.—A, Young indusium of *Goodenia paniculata* Sm. l.s. $\times 160$. B, Young indusium of *G. paniculata* showing cell divisions in upgrowth. $\times 320$. C, Stylar hair of *Campanula*. $\times 160$. D, Pseudoindusium of *Lobelia alata* Labill., stamens cross-hatched. $\times 80$.

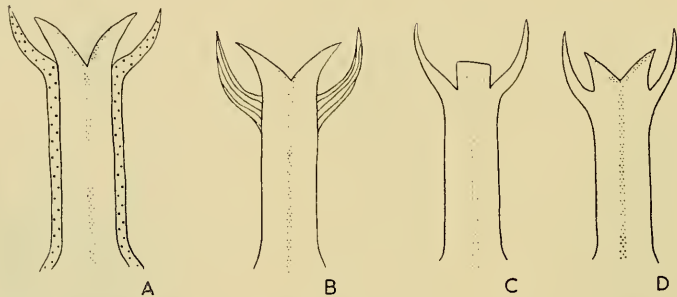
Dampiera (Text-fig. 2, M). In this group of genera the indusium first develops as distinct flaps of tissue on either side of the style and somewhat below the summit (Text-fig. 2, A-D). As in *Dampiera* the inner cells of the indusium are developed from both epidermal and subsurface layers (Text-fig. 3, A and B).

It should be noted that the stigmatic areas in all these genera, except *Leschenaultia*, are limited to the uppermost parts of the outgrowth from the floor of the indusium. Pollen grains do not germinate if they are merely in contact with the sides of this column (Text-figs 1, C-D, and 5).

The indusium of this family has attracted much speculation and several interpretations have been put forward, based on macroscopic appearance. Brown (1818) suggested that the indusium is derived from the upgrowth of an epigynous (or hypogynous) disc which he supposed to be modified stamens. He then draws a parallel

between this indusium and the anther lobes of the Stylidiaceae, especially the female flowers of *Phyllachne*. This system of homologies is incomplete and confused. Applying the phylogenetic concept to these suggestions there are two separate ideas: (i) a nectary, modified from stamens which the nectary no longer resembles, has grown up and enclosed the style, and (ii) anthers have been modified to form an indusium.

With regard to (i) it would be difficult to eliminate it completely. But first there is a nectary still present in the Goodeniaceae and situated well below the style (Carolin, 1959), and secondly there is no differentiation of an outer layer to the style which may correspond to the upgrown nectary. Thus this derivation seems unlikely. With regard to (ii) one must go rather further than Brown. It must be postulated that the ancestors of both the Stylidiaceae and Goodeniaceae had two whorls of stamens, one whorl with a tendency towards adnation to the style. In the former family the free whorl has been lost, whereas in the latter the inner whorl has been modified into the indusium. But if *Donatia* is included in the Stylidiaceae this seems to be ruled out as it has only one whorl of free stamens and no indusium. In addition the indusium bears no structural relationship to an anther and a more satisfactory explanation can be found elsewhere. Goebel (1899) modified Brown's theory and considered the indusium to be an upgrowth from the receptacle (Text-fig. 4, A).

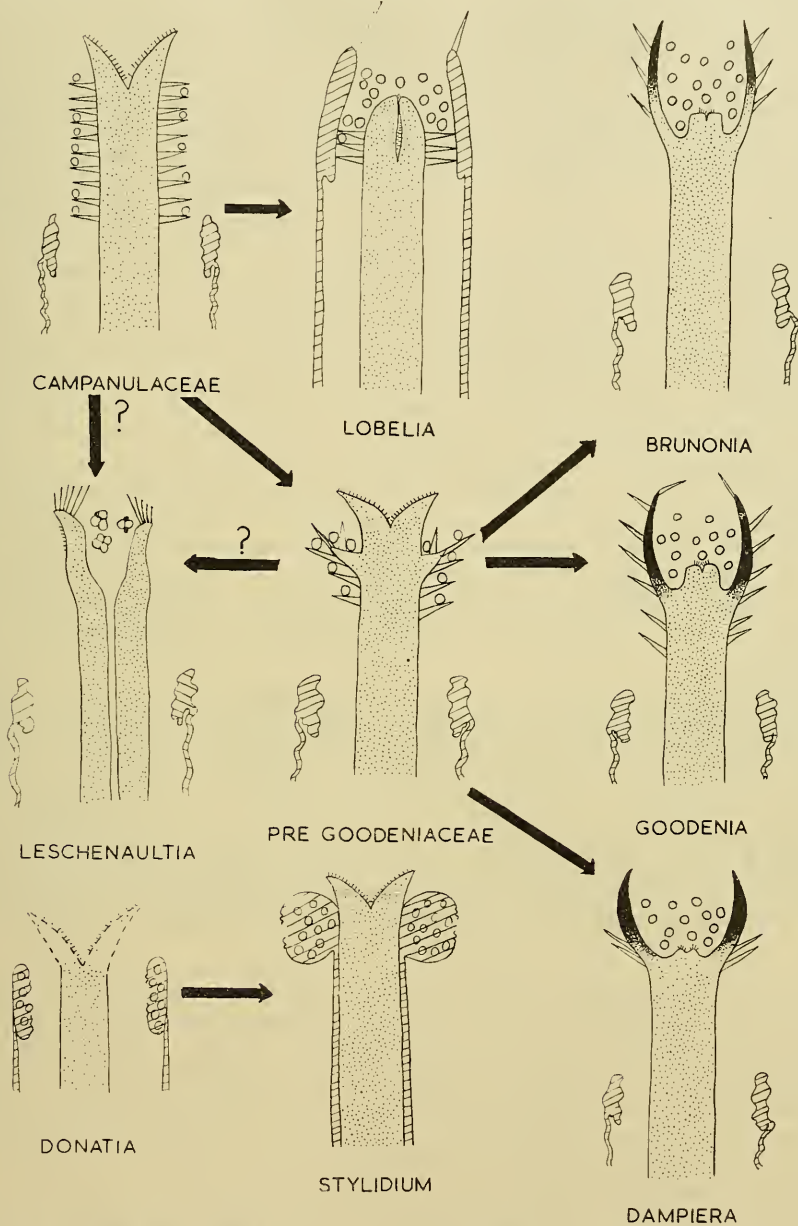


Text-fig. 4.—Interpretations of indusial structure: A, Brown, modified by Goebel; B, Lindley; C, Hanf; D, Author.

Lindley (1836) based his ideas on a rather more rigid system of logic. He suggested that the indusium consisted of a ring of hairs (as found in Lobelioideae) consolidated into a cup (Text-fig. 4, B). His thinking, however, was strictly typological and not phylogenetic. There are a number of reasons why the Lobelioideae cannot be the direct ancestors of the Goodeniaceae (Carolin, 1959), and from both typological and phylogenetic angles the indusium cannot be morphologically equivalent to the pollen collecting hairs of the Campanulaceae. If it were so, one would expect the indusium to consist of a series of elongate cells, continuous from base to the top, and the hairs projecting from it to be simply continuations of these cells. In addition one would expect the epidermis, as such, not to be continuous over the surface of the indusium, and the inner cells of the indusium to be derived from the epidermal cells of the young style as are the stylar hairs in Campanulaceae (Text-fig. 3, C). In fact none of these conditions are fulfilled (see above).

Hanf (1936) has put forward another view after extensive investigations of stylar structure in a number of families. In effect he suggests that the stigmatic surface, i.e., the external part of the pollen-transmitting tissue, is restricted to the notch between the stylar branches. The indusium then consists of the sterilized upper parts of these branches. Hanf's general interpretation of stylar structure has received some confirmation from the investigations of the carpels of the Magnoliales (Bailey and Swamy, 1951). If Hanf's views were sound in this case, one might expect to find vascular tissue in the indusium as in most stylar branches and also, as his own figures indicate, that the whole floor and/or column of the indusium would be stigmatic. As has been stated before, this is not so (Text-fig. 4, C).

The structures within the indusium correspond exactly to a normal style with rather reduced stigmatic branches which are usually separated by a cleft which may, or may not, correspond to the pseudocarpels (Text-figs. 1, 2, 5). Thus this structure can be considered as a continuation of the style proper. The indusium would then be simply



Text-fig. 5.—Phylogenetic scheme to show modifications of the pollen presentation structures in the Campanales (||||| stigmatic surface).

an outgrowth of the style. Although the cells of the indusium have thickened walls, this is presumably an adaptation to make the indusium more rigid and, therefore, more efficient in collecting the pollen. In some cases there are echoes of a 4-partite constitution to the indusium, which may be related to the postulated primitive condition of the

ovary (Carolin, 1959). The hairs on the indusium provide further evidence for its stylar nature. Those at the margin may perform the same function as the hairs of the anther apex of Lobelioideae, but the evidence for rejecting the anther origin of this structure has been given above.

Leschenaultia is, in this respect as in others (Carolin, 1959), anomalous. Indeed Bentham (1869) has suggested that the upper lip of the indusium is stigmatic in origin and that the true indusium is represented by the lower lip and the hairs at the base of the upper lip. One would then expect the pollen-transmitting tissue (or in this case the stylar canal) to pass down the centre of the upper lip, which it does not do (Text-fig. 1, A). It is true that in the species which were examined the "stigmatic" surface is limited to the upper lip between the pollen brush and the stiff hairs at the base of the lip, but the position of the stylar canal precludes Bentham's explanation. It is possible that a transference of function has taken place here, the stigmata in *Leschenaultia* being represented by the two large protuberances at the base of, and inside, the indusium (seen particularly well in *L. formosa*, Plate ii). These, apparently, no longer function and certain cells on the external surface of the upper indusial lip have taken over the stigmatic function. Pollen grains are often capable of germinating in any sugary fluid, as shown by those that accidentally fall into the nectary and germinate there. Thus, if conditions are provided elsewhere for pollen germination in such a position that fertilization can take place, the stigmata, in the morphological sense, may be dispensed with. The selective factor operating to produce this transference of function could only be indicated by a greater knowledge of the biological functioning of the flower. The pollen being actually in contact with the stigmata of the same flower, as in most Goodeniaceae, may provide for a greater probability of self-pollination than in *Leschenaultia* where the functional stigmatic surface is not in contact with pollen from the same flower, unless placed there by some external agency. The breeding system of *Leschenaultia* would appear to be one orientated essentially to outbreeding; the other genera may have higher probabilities of self-fertilization.

STYLIDIACEAE.

In the Stylidiaceae the situation is scarcely comparable at all. Brown's comparison has been dealt with above. In all cases in this family the pollen is presented to visiting insects whilst still contained within the anther lobes (Text-fig. 5). Thus the method of presentation is quite different from that of the previous two families, although the position of the structures involved is the same. Even in *Donatia*, in which the stamens are virtually free from the style, the pollen is not deposited on the style until pollination. In none of these species are there pollen-collecting hairs. Indeed, with regard to these characters, the key ones for the Order, the Compositae stand closer to the Campanulaceae than either of the other two families considered here.

GENERAL CONCLUSIONS.

The results described here provide further evidence for questioning the naturalness of the Order. Homology, i.e., morphological equivalence, has become the test of phylogenetic relationship and the pollen presentation structures of the three families considered above are not, strictly, homologous. The Stylidiaceae stand quite apart in this respect, and to this considerable difference must be added those previously noted (Carolin, 1960). It seems even more imperative now to make a detailed comparison between Campanulaceae—Stylidiaceae—Saxifragaceae.

Even the Goodeniaceae appear to be much less closely related to the Campanulaceae than most authors have previously thought. The Lobelioideae mechanism is directly derivable from that found in *Campanula* (see above); that of the Goodeniaceae is not.

The indusium has been shown to be not homologous with the stylar hairs of Campanulaceae (see above). It has also been noted that hairs, similar in structure to those of the latter family, are found on the indusia of *Brunonia* and the *Goodenia* group of genera. In the latter these hairs are often concentrated on the lips and function as a pollen-brush (Hamilton, 1894, 1895). Although these hairs show little difference from

normal epidermal hairs, they are seldom found on the styles of members of other Orders, and even then they do not usually function as a pollen-brush (but excepting Asterales). Thus the pollen-presentation function, in this case, is carried out by an entirely new structure, an outgrowth from the style. The pollen-collecting hairs perform an ancillary function, i.e., that of brushing pollen *into* the indusium and providing stiff structures with which the visiting insects agitate the indusium, thus releasing the pollen. In *Dampiera* these hairs appear to have disappeared completely for reasons which are not apparent.

The indusium of *Leschenaultia* is probably derived from the condition found in *Goodenia*, but, physiologically at least, is very different. To this considerable difference must be added the anomalous vasculature of the flower (Carolin, 1959) and the formation of mature, segregating pollen tetrads (Martin and Peacock, 1958), a condition unknown elsewhere in the family.

It is difficult to analyse the characters which have influenced systematists in grouping Goodeniaceae with Campanulaceae. As Rendle (1938) has pointed out, the main factor has been pollen presentation, but the general resemblance of the flower to that of the Lobelioideae must also have played a large part; in this case resemblance must be largely a result of convergence. Lindley's hypothesis has been dealt with above. There are members of both Lobelioideae and Goodeniaceae without the slit in the corolla-tube; in those Lobelioideae with bilocular ovaries the vasculature is consistent with a bicarpellary structure, whereas in the Goodeniaceae it is not (Carolin, unpub., 1959); the connation of the anthers in the two families has also arisen separately if the monophyletic origin of the Goodeniaceae is accepted. This general floral resemblance, then, is not a direct result of common ancestry. In addition Colozza (1908) notes that there are anatomical differences between the two families. Rosen's results with regard to embryology are inconclusive (Rosen, 1946).

There seems little else to go on at present, but for these parallel changes and the single, tenuous, structural, homologous link of the pollen-collecting hairs and the functional link of pollen presentation. More data are very necessary, particularly from the point of view of anatomy and biochemistry, but at present the following conclusions of taxonomic importance may be drawn: (i) that the Order, as designed by Hutchinson, is probably unnatural (particularly is this true of the inclusion of the Stylidiaceae); (ii) that the Asterales are probably more closely related to the Campanulaceae than are the Goodeniaceae.

In considering the general functioning of these structures the Stylidiaceae represent the primitive condition. In the vast majority of flowering plants pollen is presented to insects whilst still contained in anther lobes. The actual advantage in transferring this function to the naked style, as has occurred in the Campanulaceae, is not at all clear. Presumably it is that pollen is deposited upon the insect in such a position that the stigmatic lobes in an older flower will be in the exact position to receive it. The turning point of the mechanisms in all three families is the sequential presentation of first mature pollen and then mature stigma in the same position of the same flower but at different times. Indeed, this sequential presentation is of considerably wider occurrence than the Campanales, although in most families it is brought about by movements, growth or otherwise, of the stamens and style (e.g., Labiatae, Scrophulariaceae, Solanaceae, etc., see Knuth, 1909). What is fairly clear, however, is, once the "naked" method of pollen preservation was fixed, there appears to have been certain advantages in reverting to a "closed" method. The probability of a complete reversion in evolution is very low indeed, and in any case there were probably selective factors operating to maintain the presentation function upon the style. The consequence has been that new functional units have developed upon the style, or directly associated with the style, in which pollen is contained. Different evolutionary lines have developed different morphological units to perform the same function of pollen protection, the general tendency being that these structures release pollen only when deposition upon an insect is more or less assured. Thus there is the corolla-style pseudo-indusium of

Phyteuma, the anther-style pseudo-indusium of Lobelioideae, and the stylar indusium of Goodeniaceae. All of these structures may be correlated, to a greater or lesser degree, with the pollen collecting hairs of *Campanula*; the Styliaceae occupy no position in this scheme, their structures showing more resemblance to those of other Orders.

The trend, then, has been first sequential presentation and subsequent pollen protection. This protection may operate against unwanted pollinators, but detailed observations on insect visitors and breeding systems in some of the species concerned are needed before this can be considered as anything more than a suggestion. It is interesting to note, however, that the Campanulaceae, with their naked presentation, are considerably commoner in drier than in damp areas and it may be under such conditions that they first developed. The development of pollen-protective devices may have been correlated with an extension into damp temperate regions—a protection against rain or other factors in the physical environment. This might even mean a temperate origin for the Goodeniaceae; a re-entry into dry tropical conditions would not necessarily mean a reversion to “naked” presentation.

I am indebted to Professor N. S. Bayliss, Professor C. L. Wilson and Mr. W. J. Peacock for supplying some of the specimens used in this investigation. The collection of the rest of the material was made possible by a grant from the University of Sydney Research Fund.

VOUCHER SPECIMENS EXAMINED.

Velleia paradoxa R.Br., Armidale, N.S.W., R. Carolin, 11.1956. SYD. *V. lyrata* R.Br., Mt. White, N.S.W., W. J. Peacock, 15.11.1958. SYD. *V. macrocalyx* R.Br., Bowen's Creek, Bilpin, N.S.W., R. Carolin, 20.11.1958. SYD. *Goodenia paniculata* Sm., La Perouse, Sydney, N.S.W., W. J. Peacock, Feb. 1958. SYD. *G. bellidifolia* Sm., Kanangra Tops, N.S.W., R. Carolin, no. 462, 5.4.1958. SYD. *G. ovata* Sm., Kuring-gai Chase, N.S.W., W. J. Peacock, 10.1958. SYD. *G. decurrens* R.Br., Blackheath, N.S.W., R. Carolin, 10.1956. SYD. *Selliera radicans* Cav., Concord, N.S.W., R. Carolin, Sept. 1956. SYD. *Scaevola ramosissima* (Sm.) Krause, Bowen's Creek, Bilpin, N.S.W., R. Carolin, 20.11.1958. SYD. *S. albida* (Sm.) Druce, Concord, N.S.W., R. Carolin, Sept. 1956. SYD. *Verreauxia reinwardtii* (De Vr.) Benth., Lime Lake, Wagin, W.A., N. T. Burbidge, no. 4956, 28.12.1955. CANB. *Leschenaultia formosa* R.Br., University Garden. *L. biloba* Lindl., C. L. Wilson, W.A. No voucher. *L. linarioides* DC., C. L. Wilson, W.A. No voucher. *Dampiera stricta* R.Br., Kuring-gai Chase, N.S.W., W. J. Peacock, Oct. 1958. SYD. *D. purpurea* R.Br., Church Point, Sydney, N.S.W., W. J. Peacock, Oct. 1958. SYD. *D. linearis* R.Br., C. L. Wilson, W.A. No voucher. *Brunonia australis* R.Br., Bell, N.S.W., R. Carolin, no. 607, 20.11.1958. SYD. *Campanula rotundifolia* L., West Lebanon-Plainfield, N. Hants, U.S.A., C. L. Wilson, 17.7.1958. SYD. *Wahlenbergia trichogyna* Stearne, Kanangra-Jenolan, N.S.W., R. Carolin, no. 462, 6.4.1958. SYD. *Specularia speculum* L., Botanischer Garten, Köln. SYD. *Phyteuma orbiculare* L., Botanischer Garten, Köln. SYD. *Lobelia alata* Labill., Marley Beach, National Park, N.S.W., R. Carolin, Oct. 1956. SYD. *L. gracilis* R.Br., Berowra, N.S.W., R. Carolin, 11.1958. SYD. *Laurentia petraea* F. Muell., Floods Creek, Fowlers Gap, N.S.W., R. Carolin, no. 331, Aug. 1957. *L. fluviatilis* (R.Br.) Wimm., Geehi River, R. Carolin (died before preservation, no voucher). *L. syphilitica* L., Private Garden. SYD. *Stylidium graminifolium* Swartz, Oatley, W. J. Peacock, Jan. 1958. SYD. *Donatia nova-zealandiae* (Hook. f.) Berg., collected by Prof. Bayliss. No voucher.

Bibliography.

- BAILEY, I., and SWAMY, B. G. L., 1951.—The Conduplicate Carpel of the Dicotyledons and its Initial Trends in Specialization. *Amer. Journ. Bot.*, 38: 373.
- BENTHAM, G., 1869.—Notes on the Stigmatic Apparatus of the *Goodenovieae*. *Journ. Linn. Soc. Lond. Bot.*, 10: 203.
- BRONGNIART, A., 1839.—Sur les Poils Collecteurs des Campanules etc. *Ann. Sci. Nat. Bot.*, ser. 2, 12: 244.
- BROUGH, P., 1927.—Studies in the Goodeniaceae. i. The Life History of *Dampiera stricta* R.Br. *PROC. LINN. SOC. N.S.W.*, 52: 471.
- BROWN, R., 1818.—Some Observations on the Natural Order called *Compositae*. *Trans. Linn. Soc. Lond.*, 12: 134.
- CAROLIN, R. C., 1959.—Floral Structure and Anatomy in the family Goodeniaceae Dumort. *PROC. LINN. SOC. N.S.W.*, 84: 242.
- CAROLIN, R. C., 1960.—Floral Structure and Anatomy in the family Styliaceae. *PROC. LINN. SOC. N.S.W.*, 85: 189-196.
- DARWIN, C., 1871.—On the Fertilization of *Leschenaultia*. *Gard. Chron.*, 1871; 1166.
- GOEBEL, K., 1899.—*The Organography of Plants*. Oxford.

- HAMILTON, A. G., 1894, 1895.—Notes on the Methods of Fertilization of the Goodeniaceae. *Proc. Linn. Soc. N.S.W.*, 9: 201; 10: 361.
- HASSALL, A. B., 1842.—Observations on the function performed by the Hairs on the Stigma in *Campanulaceae*, *Compositae* and other plants. *Ann. Mag. Nat. Hist. Lond.*, 8: 84.
- HANF, M., 1936.—Vergleichende und entwicklungsgeschichtliche untersuchungen über Morphologie und Anatomie der Griffel und Griffeläste. *Beihefte Bot. Centr.*, 54: 99.
- HUTCHINSON, J., 1926.—*Families of Flowering Plants*. Vol. I. London.
- KNUTH, P., 1909.—*Handbook of Flower Pollination*. Vol. III; trans. J. R. Ainsworth Davis.
- KRAUSE, K., 1912.—*Das Pflanzenreich—Goodeniaceae und Brunoniaceae*. Berlin.
- LINDLEY, J., 1836.—*A Natural System of Botany*. Ed. 2. London.
- MARTIN, P. G., and PEACOCK, W. J., 1959.—Pollen Tetrad Patterns in *Leschenaultia*. *Proc. Linn. Soc. N.S.W.*, 84: 271.
- RENDLE, A. B., 1938.—*The classification of Flowering Plants*. Vol. 2. Cambridge.
- ROSEN, W., 1946.—Further notes on the Embryology of the Goodeniaceae. *Acta Hort. Gotöb.*, 16: 235.

EXPLANATION OF PLATE II.

1. *Scaevola calendulacea*.—l.s. of young indusium, stigmatic cleft just appearing.
2. *Dampiera linearis*.—l.s. of mature indusium showing young, stigmatic cleft.
3. *Leschenaultia formosa*.—l.s. of mature indusium; the cubical, papillose cells with prominent nuclei situated on the upper lip represent the functional stigmatic surface.
4. *Wahlenbergia trichogyna*.—t.s. of young style showing position of pollen-collecting hairs.